

The role of semelparity, delayed reproduction and density dependence on population dynamics

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ABSTRACT

Several factors affect the dynamics of species population. Some of them come from human activities, some from environmental conditions and others are inherent to the species themselves. The current study attempted to measure the effect of semelparity, delayed reproduction and density dependence on the asymptotic and transient growth rates of a subshrub plant species. We found that the growth rate of subshrub species is favored by adults when increasing the survival rate and maturation process. Meaning that the delayed reproduction and slow speed of maturity decrease the population growth rate.

Key words: subshrub, semelparity, iteroparity, transient, delayed reproduction, density-dependent, elasticity.

INTRODUCTION

Population ecology studies the causes, processes and consequences of variation in the numbers of individuals within natural populations. One important challenge is to understand the factors and mechanisms that drive population size and how, in this respect, populations cope with time-varying environments? (Acker et al 2014).

Many of officially published papers have developed the aspect that some demographical activities such as harvest (Gaoue & Tamara, 2010) and environmental conditions, very investigated in species habitat modeling like in Moyo et al. 2019, impact the species population dynamic spatially and temporally. However, they are also some factors linked to the species themselves, which affect the dynamic of their population.

The current study focuses on the role of semelparity, delayed reproduction and density dependence on population dynamics of a subshrub plant species. Three relevant questions will be answered. Firstly, what is the evolution of growth rate in a population of subshrub species while the maturation rhythm change across time? Secondly, what is the evolution of growth rate in a population of subshrub species while the survival rate of adult reproductive individuals change across time? The answer to this question will help us to state whether semelparity life history can be selected for. Finally, what is the evolution of growth rate for semelparous and iteroparous while the over-compensatory density dependence change across time?

MATERIALS AND METHODS

MATERIALS

This work is based on the exam sheet provided by Prof. Orou Gaoué, as protocole to conduct the study. All the simulations have been done in software R version 4.0.5 (2021-03-31) and the database generated was stored in MS Excel.

METHODS

Model design

A subshrub species is a small woody plant. We can find example of *Banisteriopsis campestris* in Pereira et al., 2020. Generally, they are less tall.

In short, the Life-cycle of a subshrub species can be resumed in two compartments as following (**Figure 1**):

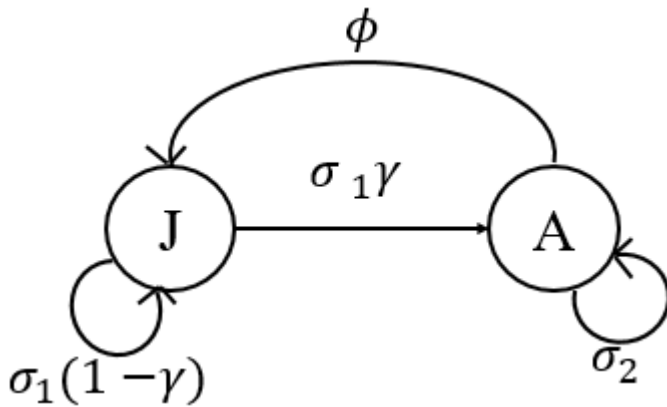


Fig 2: live cycle of a two-stage model with stage 1 (J) for juveniles and stage 2 (A) for adults. Arrows indicate possible contributions of one stage to the other. σ_1 : annual survival rate of juveniles, γ : annual maturation rate, σ_2 : annual survival rate of adults, and ϕ : annual fertility rate.

From the live cycle, we can draw the system of difference equations representing the matrix projection model:

$$\begin{cases} J(t+1) = \sigma_1(1-\gamma)J(t) + \phi A(t) \\ A(t+1) = \sigma_1\gamma J(t) + \sigma_2 A(t) \end{cases} \quad (\text{Eqn: 1})$$

$$\begin{bmatrix} J(t+1) \\ A(t+1) \end{bmatrix} = \begin{pmatrix} \sigma_1(1-\gamma) & \phi \\ \sigma_1\gamma & \sigma_2 \end{pmatrix} \begin{bmatrix} J(t) \\ A(t) \end{bmatrix} \quad (\text{Eqn: 2})$$

Hence we get, the following 2×2 projection matrix A which represent the demographic transitions for a subshrub plant species.

$$A = \begin{bmatrix} \sigma_1(1-\gamma) & \phi \\ \sigma_1\gamma & \sigma_2 \end{bmatrix}$$

In the matrix A , γ is bounded between zero and one and describe the maturation process. Species for which γ has large values are characterized by rapid maturation process (precocious development). In contrast, species with small values for γ have slow maturation process and therefore delay reproduction. σ_2 is also bounded between zero and one and represents the survival rate of adult reproductive individuals. Consequently, species with small values of σ_2 tend to be semelparous because in this case adults are less likely to reproduce more than once given their low survival probability. However, species with large σ_2 have long-lived adults and are therefore iteroparous. ϕ represents the fertility, the mean number of offspring produced by adults.

Analysis

The analysis is split into three parts:

Effects of delayed reproduction on the asymptotic (λ_0) and transient (λ_1) dynamics

Here, we assumed that $\sigma_1 = 0.5$, $\sigma_2 = 0.9$, $\phi = 1.5$ only γ vary across time. Using matrix A , we modeled the behavior of the asymptotic (λ_0) and transient (λ_1) dynamics while varying γ .

Effects of iteroparity on the asymptotic (λ_0) and transient (λ_1) dynamics

Now, we assumed that $\sigma_1 = 0.5$, $\gamma = 0.1$, $\phi = 1.5$ and only σ_2 . And using matrix A , we modeled the behavior of the asymptotic (λ_0) and transient (λ_1) dynamics while varying σ_2 .

Effect of over-compensatory density dependence on the asymptotic (λ_0) and transient (λ_1) dynamics

Negative density dependence is an important process that can alter population dynamics. Density dependent projection matrix are written as a function of the total population size N : $A(N)$. Density dependence is often modeled using Beverton Holt function ($\frac{1}{N+1}$) to capture compensatory density dependence and Ricker function (e^{-N}) to illustrate over-compensatory density dependence.

Here, we assumed that density dependence affects only fertility ϕ and used A ($\sigma_1 = 0.5$, $\gamma = 0.1$ and $\phi = 1.5$) to simulate the effect of over-compensatory density dependence on the asymptotic and transient population dynamics for semelparous ($\sigma_2 = 0.1$) and iteroparous ($\sigma_2 = 0.9$) species.

This means that we have answered to the question:

How do we actually assess the growth dynamics?

Asymptotic (λ_0) dynamic:

To get the asymptotic (λ_0) dynamics, we have recoded all the asymptotic values provided by the vector of each parameters (γ in first part, σ_2 in the second part and N in the third one). This value is actually the dominant eigenvalue of matrix A and represent the long-term population growth rate

(Gaoe, 2016), The behavior that a system will eventually exhibit and then retain indefinitely if unperturbed (Hastings et al., 2018).

Transient (λ_1) dynamic:

Transient dynamic is nonasymptotic dynamic (Hastings et al., 2018). Following Gaoe, 2016, we used the average transient growth rate $\lambda_1(p_1, p_2)$ as the metric of transient dynamics to facilitate comparisons with the long-term growth rate, λ_0 . Were p_1 and p_2 stand for parameters (γ in first part, σ_2 in the second part and N in the third one) at two different levels. We keep that:

$$\lambda_1(p_1, p_2) = \lambda_1 = \frac{1}{p_1 - p_2} \log \frac{\lambda_0(p_2)}{\lambda_0(p_1)} \quad (Eqn: 3)$$

The transient dynamics rather than long-term behavior in ecological systems, enable the examination of forces that allow coexistence on short timescales (Hastings et al., 2018).

Elasticity:

The elasticity of λ_0 measures the proportional change to population growth rate as a response of proportional perturbation. Perturbations in our case, are semelparity, delayed reproduction and density dependence of species).

Elasticity comes out as matrix different process of the species. For this study, we just have a 2×2 matrix, then the elasticity matrix contains four (04) element. To get information about the elasticities, we compute the arithmetic mean value of each components (Elast1.1, Elast1.2, Elast2.1, and Elast2.2).

Elasticity table 0

	J	A
J	Elast _{1.1}	Elast _{1.2}
A	Elast _{2.1}	Elast _{2.2}

The containing 5 entries of each dataset can be seen in Appendix S2.

RESULTS

The asymptotic growth rate increases with the speed of the maturation process and shows a downward concavity. But the transient dynamic reveal that when the maturation rate lie between 0 and 20%, the growth rate increase considerably and start to decrease with an upward concavity after 20% of maturity rate. (Fig. 1).

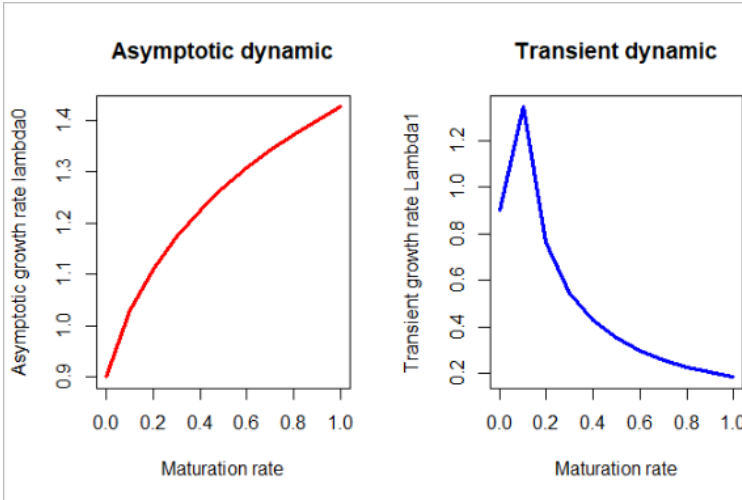


Fig 2: Asymptotic and transient dynamics given the maturation rates

Like in **Fig 2**, the asymptotic growth rate increases with the speed of the survival rate and shows an upward concavity. But the transient growth rate reveal that when the survival rate is null, the population size come down to zero. The transient growth rate increases when the survival rate increases up to the pic (around 70%) and after the pic of survival rate, the transient growth rate decrease (**Fig 3**).

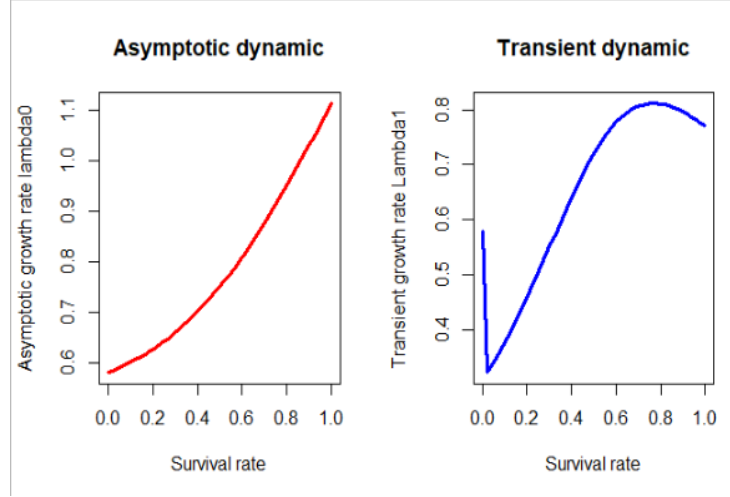


Fig 3: Asymptotic and transient dynamic given survival rate

In a semelparous population, when the over-compensatory density increase inside the interval of $[1; 4]$ times, the asymptotic growth rate decreases before being stable a 0%. The transient dynamic reveal that, in fact, at this decreasing period the growth rate go under zero. (**Fig.4**). After 10 times increasing in over-compensatory density, we can see no movement in the population density. The growth rate is zero (**Fig. 5**).

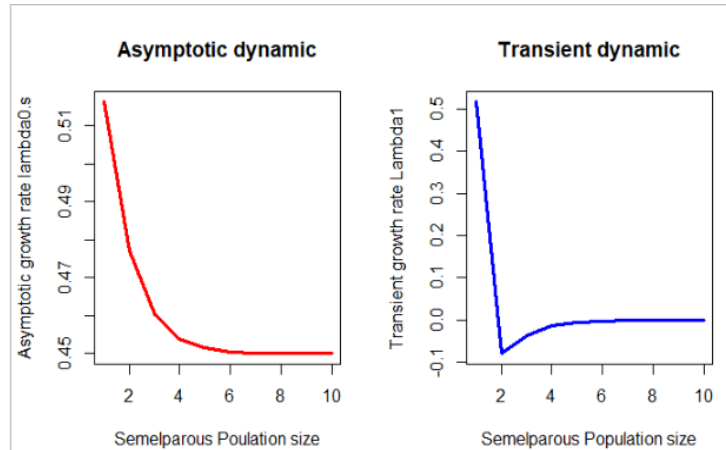


Fig 4: Asymptotic and transient dynamics in function of over-compensatory density (1 to 10 times increase) in semelparous population

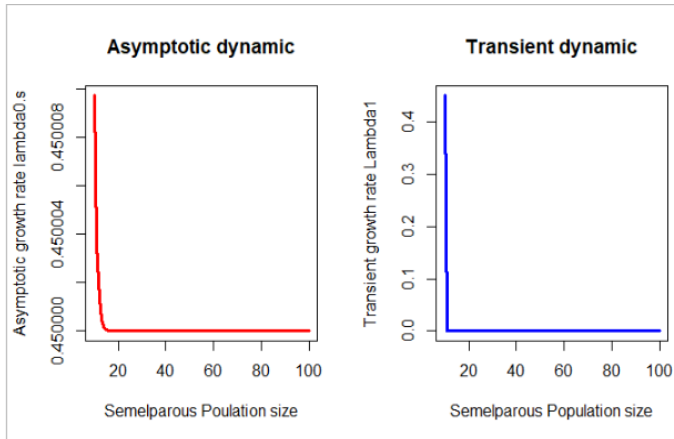


Fig 5: Asymptotic and transient dynamics in function of over-compensatory density (10 to 100 times increase) in semelparous population

Fig.6 and **Fig.7** show the same result for iteroparous as for semelparous.

Concerning elasticities,

the effect of maturation process yield the following mean elasticity values:

Elasticity table 1

	J	A
J	0,046150188	0,194903944
A	0,194903944	0,564041925

The effect of survival rates yield the following mean elasticity values:

Elasticity table 2

	J	A
J	0,303741998	0,162897778
A	0,162897778	0,370462446

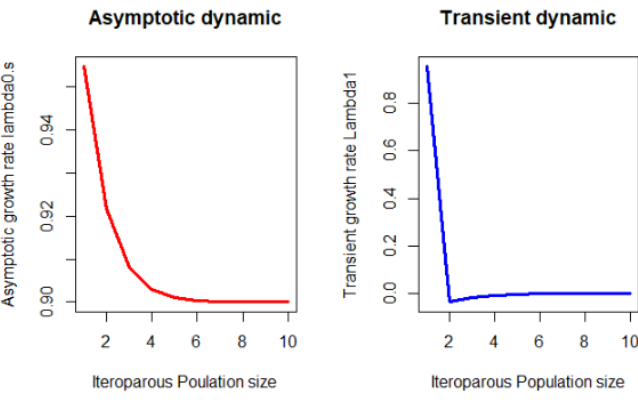


Fig 6: Asymptotic and transient dynamics in function of over-compensatory density (1 to 10 times increase) in iteroparous population

The effect of over-compensatory density dependence in semelparous population yield the following mean elasticity values:

Elasticity table 3

	J	A
J	0,999999	3,76E-07
A	3,76E-07	1,07E-07

The effect of over-compensatory density dependence in iteroparous population yield the following mean elasticity values:

Elasticity table 4

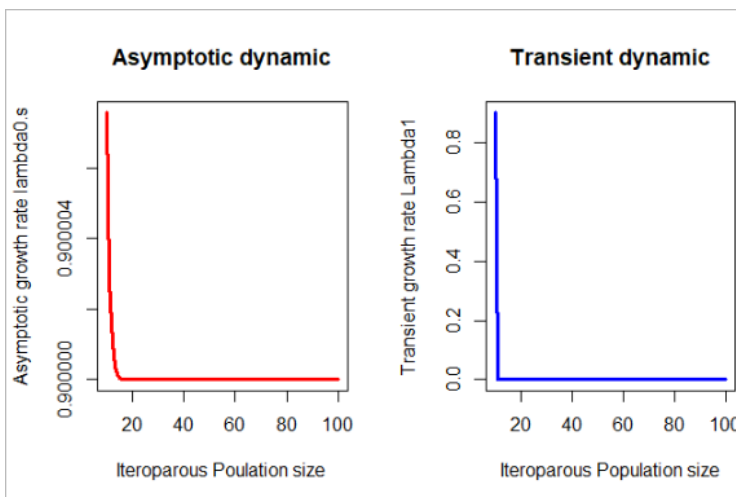


Fig 7: Asymptotic and transient dynamics in function of over-compensatory density (10 to 100 times increase) in iteroparous population

	J	A
J	1,46151E-07	1,46E-07
A	1,46E-07	1

DISCUSSION

Regarding elasticities (**Elasticity table 1 and Elasticity table 2**), we deduce that to increase the population growth rate we should increase the maturation rate and survival rate of adults. But in the case of over-compensatory density-dependence, juvenals semelparous can help to increase the population growth rate while the adults keep the rate for iteroparous. Meaning that the delayed reproduction and slow speed of maturity decrease the population growth rate.

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DATA ACCESSIBILITY

Appendix S1

The R script used to simulate the effect of delayed reproduction, iteroparity and over-compensatory density dependence on the asymptotic (λ_0) and transient (λ_1) dynamics of population growth rates is available from GitHub at:

<https://github.com/luc-z/Population-dynamic-modeling-effect-of-delayed-reproduction-iteroparity-and-density-dependence.git>

Appendix S2

Maturation rate

maturation.proces s	Lambda0	Lambda1	Elast_1.1	Elast_1.2	Elast_2.1	Elast_2.2
0	0,9	0,9	0	0	0	1
0,020408163	0,93442451 2	1,83926799 3	0,03766648 3	0,03419300 7	0,03419300 7	0,89394750 2
0,040816327	0,96328815	1,49066543 4	0,05760537 1	0,05809837 3	0,05809837 3	0,82619788 3
0,06122449	0,98846203 5	1,26408471 4	0,06914431	0,07646350 5	0,07646350 5	0,77792868

Survival Rate

Survival.rate	Lambda0	Lambda1	Elast_1.1	Elast_1.2	Elast_2.1	Elast_2.2
0	0,579436172	0,579436172	0,634811054	0,182594473	0,182594473	0
0,020408163	0,583251904	0,321619422	0,623842952	0,184729469	0,184729469	0,00669811
0,040816327	0,587252894	0,334982414	0,612446585	0,186800147	0,186800147	0,013953121
0,06122449	0,591449407	0,348909164	0,600615173	0,188792578	0,188792578	0,021799672
0,081632653	0,595852121	0,363402175	0,58834423	0,190691675	0,190691675	0,030272419

Over-compensatory density for semelparous

Pop. Size	Lambda0.s	Lambda1.s	Elast_1.1	Elast_1.2	Elast_2.1	Elast_2.2
10	0,45001	0,45001	0,999951	2,16E-05	2,16E-05	6,18E-06
11	0,450004	-1,4E-05	0,999982	7,95E-06	7,95E-06	2,27E-06
12	0,450001	-5E-06	0,999993	2,93E-06	2,93E-06	8,36E-07
13	0,45	-1,8E-06	0,999998	1,08E-06	1,08E-06	3,08E-07
14	0,45	-6,8E-07	0,999999	3,96E-07	3,96E-07	1,13E-07

Over-compensatory density for iteroparous

Pop. Size	Lambda0.i	Lambda1.i	Elast_1.1	Elast_1.2	Elast_2.1	Elast_2.2
10	0,900007567	0,900007567	8,4069E-06	8,41E-06	8,41E-06	0,999975
11	0,900002784	-5,31433E-06	3,09284E-06	3,09E-06	3,09E-06	0,999991
12	0,900001024	-1,95507E-06	1,13781E-06	1,14E-06	1,14E-06	0,999997
13	0,900000377	-7,19235E-07	4,18578E-07	4,19E-07	4,19E-07	0,999999
14	0,900000139	-2,64592E-07	1,53987E-07	1,54E-07	1,54E-07	1

Moyo, Sithabile, et al. "Spatial distribution and abundance of the African baobab (*Adansonia digitata*) in Zimbabwe." *Transactions of the Royal Society of South Africa* 74.3 (2019): 213-218.

Pereira, Cássio Cardoso, et al. "Are extrafloral nectaries efficient against herbivores? Herbivory and plant defenses in contrasting tropical species." *Journal of Plant Ecology* 13.4 (2020): 423-430.

REFERENCE

Acker, Paul, et al. "Heterogeneity of reproductive age increases the viability of semelparous populations." *Functional Ecology* 28.2 (2014): 458-468.

Hastings, Alan, et al. "Transient phenomena in ecology." *Science* 361.6406 (2018).

Gaoue, Orou G. "Transient dynamics reveal the importance of early life survival to the response of a tropical tree to harvest." *Journal of Applied Ecology* 53.1 (2016): 112-119.

Gaoue, Orou G., and Tamara Ticktin. "Effects of harvest of nontimber forest products and ecological differences between sites on the demography of African mahogany." *Conservation Biology* 24.2 (2010): 605-614.

Hastings, Alan. "Transients: the key to long-term ecological understanding?." *Trends in ecology & evolution* 19.1 (2004): 39-45.